Temporal and spatial segregation of *Battus devilliers* and *B. polydamas cubensis* (Papilionidae) in La Habana, Cuba

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Abstract. The spatial and temporal distribution of two syntopic species of the genus *Battus* (Papilionidae) that inhabit two areas in the north coast of La Habana, Cuba, is analyzed. The study was carried out from April 2006 to March 2007. Samples were taken using transects 100 m long, separated from each other by 80 m gaps. Populations of *B. polydamas cubensis* and *B. devilliers* of the evergreen forest at Boca de Canasí, the most natural habitat, had similar abundance, while in the secondary scrub at Boca de Jaruco, an extremely degraded area, *B. polydamas cubensis* was much more abundant than *B. devilliers*. Analysis of structural subniche usage by season showed significant differences in daily activity (from 9:00 am to 12:00 m and from 12:00 m to 3:00 pm) and habitat type for each species. Flight stratum had lesser influence than sunlight intensity on both butterflies. Populations of the latter seemed to be influenced by seasonality, while those of *B. polydamas cubensis* seemed more influenced by habitat.

Key words: *Battus*, Cuba, Papilionidae, segregation, syntopic species.

INTRODUCTION

Ecological roles of butterflies are important for ecosystems functioning, with their study needed to better understand their ecological interactions and functions. In Cuba, only Fontenla (1989) and Genaro *et al.* (1994) have conducted studies focusing on butterflies communities and their resource partitioning in a particular habitat. Due to their rapid reproduction and close association with specific physical factors and plant resources butterflies are highly sensitive to environmental changes, so they are good indicators of ecosystem health (Brown, 1991; Kremen, 1992; New *et al.*, 1995; New, 1997; Brown & Freitas, 2000). *Battus* presents a Neotropical distribution (Sims & Shapiro, 1983) with 12 or 14 species (Tyler *et al.*, 1994; Racheli & Pariset, 1992, respectively). The coevolutionary association of *Battus* with their host plant, *Aristolochia* spp. (Aristolochiaceae), as well as the mimetic interactions among members of this butterfly genus may be the subject of many studies on butterfly community structure (Young, 1972, 1973).

Battus devilliers (Godart, 1823) and *B. polydamas*

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cubensis (Dufrane, 1946) are the only members of the genus that inhabit Cuba. The former occurs in Bahamas (Knowles & Smith, 1995) and the latter was reported at Cayman Islands in 1938 (Carpenter & Lewis, 1943), but there has been no recent mention of further records for these islands (Askew, 1980, 1988; Schwartz *et al.*, 1987). On several occasions (Alayón & Solana, 1989; Racheli & Pariset, 1992; Núñez & Barro, 2003) both species were recorded in Cuba as syntopic (*sensu* Rivas, 1964). The interaction becomes more interesting considering the different habitat requirements of *B. polydamas* and *B. devilliers* mentioned by Tyler *et al.* (1994), who established that *Battus polydamas* is very common in disturbed forest, while *B. devilliers* prefer more natural seasonal forest. Since resource use for both species in Cuba is completely unknown, we undertook a study of temporal and spatial patterns of two populations on the northwestern coast of Cuba.

MATERIALS AND METHODS

Study areas

The study was conducted at two localities of the north coast of La Habana. Both areas are close to human populations and show different levels of degradation. Boca de Jaruco is 45 km east of La Habana city, at 23°11' N, 82°01' W. The site is typified by secondary vegetation with many herbs and bushes and is the most impacted area, which is why the habitat is categorized

Figure 1. Study Sites. **A**: Secondary scrub of Boca de Jaruco. **B**: Sea grape forest of Boca de Canasí. **C**: Evergreen forest of Boca de Canasí. **D**: Summit of the hill where the evergreen forest canopy of Boca de Canasí becomes open.

as secondary scrub (Fig. 1a). The unique emergent large trees are isolated *Ficus* sp. (Moraceae). There are many invasive plants, the most abundant being *Acacia farnesiana* (L.) Willd., (Mimosaceae), *Comocladia dentata* Jacq. (Anacardiaceae) and members of the family Poaceae. Common species also includes *Lantana camara* L. (Verbenaceae) and *Viguiera dentata* (Cav.) Spreng., (Asteraceae), and vines as *Merremia dissecta* (Jacq.) Hallierf., (Convolvulaceae), *Cucumis dipsaceus* Ehrenb., (Curcubitaceae) and *Aristolochia bilabiata* L. During the dry season there are natural burns.

Boca de Canasí is 20 km east from Boca de Jaruco, at 23°09' N and 81°47' W. Two different habitat were analyzed there: a sea grape [*Coccoloba uvifera* (L.) L. (Polygonaceae)] forest (Fig. 1b), and an evergreen forest (Fig. 1c, d). The latter is crossed by several paths, but is less frequented by persons than the former. It also has higher relative humidity due to the cover of arboreal species such as *Bursera simaruba* (L.) Sarg. (Burseraceae) and *Coccoloba diversifolia* Jacq. that reduce incident sunlight. Endemic plants like *Coccotrinax borhidiana* O. Muñiz (Arecaceae), *Leptocereus wrightii* León (Cactaceae) and *Eugenia mollifolia* Urb. (Myrtaceae) are also common (Borhidi, 1996). On the summit of the hill (ca. 100 m above sea level) the evergreen forest canopy opens and bushes like *Acacia farnesiana* and *Croton lucidus* L. (Euphorbiaceae) are abundant.

Ecological counts

Boca de Jaruco was sampled from April 2006 to March 2007. At Boca de Canasí sampling started July 2006 in the evergreen forest, while in the sea grape habitat counts began on April 2006, ending on March 2007 and January 2007, respectively. The transect

method was followed. Individuals were counted only when seen from the sides or the front of observer, never from behind, within a range of approximately 5 m. At least once a month, eight transects were sampled each hour, from 9:00 a.m. to 3:00 p.m., at each studied site. Transect length was 100 m, the transects separated from each other by 80 m. At the end of the study a total of 992 transects in the secondary scrub of Boca de Jaruco were covered, 352 in the sea grape and 336 in the evergreen forest.

Sunlight intensity and flight stratum were recorded for each specimen. These dimensions of structural subniche were used to analyze part of the spatial segregation. Border values of each category in a particular dimension were determined following previous Cuban ecological studies on butterflies (Fontenlak, 1989; Genaro *et al.*, 1994).

For sunlight intensity three categories were defined: sunny (when individual flies directly in sunlight, without any vegetation cover), filtered sun (when individual flies under some vegetation cover, but still in sunlight) and shading (when individual flies where vegetation cover is so dense that it is difficult for sunlight to enter). Three categories of flight stratum from ground to above 3 m were defined: first level from the ground (0 - 1.5 m), second 1.5 - 3.0 m, and third > 3.0 m. When the same individual moved from one level to another only the first stratum seen was recorded. Due to variation of climate throughout the day, the two variables were analyzed separately over a two hours range, 9:00 am -12:00 m, and 12:00 m -3:00 pm.

Relative abundance was correlated with mean precipitation of the previous month. This correlation was due to both the influence of rain on vegetation and the time it takes for plant growth (rains increase flower abundance, for example). We used a correlation between these variables based on published results showing that nectar source availability is an important condition for a well developed butterfly community (Clausen *et al.*, 2001). Values of mean precipitation per month were supplied by the Instituto Nacional de Recursos Hidráulicos.

Statistical analysis

GraphPad InStat, version 3.01 (1998) software was used for data analysis. The Kolmogorov-Smirnov test was the first step in every case to evaluate data normality (p < 0.10). Median and 25 and 75 percentils were calculated. A Mann-Whitney U-test was used to compare the values of the same variable due to the nonparametric nature of data. Comparison of three or more values was performed with a Kruskal-Wallis test. When the later was significant (p < 0.05), a

Dunn's Multiple Comparisons Post-Test was applied. Correlation between two variables was analyzed with a Nonparametric Correlation (Spearman r).

Results and discussion

Spatial segregation

Habitat use. The greatest difference between populations of both species relates to their abundance in each habitat type. In the three habitats *B. polydamas cubensis* is common while *B. devilliers* is rare (Fig. 2). Human disturbance of both studied areas may be one of the factors affecting rarity, considering the habitat requirements mentioned by Tyler *et al.* (1994). Boca de Jaruco is the most disturbed site and has the highest proportional abundance of *B. polydamas cubensis* across all the sites sampled. On the other hand, the evergreen forest of Boca de Canasí is the best preserved habitat of the triad and possesses the highest proportion of *B. devilliers* individuals, even during the dry season (Fig. 3). Concerning habitat requirements, Alayón and Solana (1989) reported that both species coexist in Cuchillas del Toa, specifically in the ecotone between forest and cleared areas.

No statistical significance was found correlating precipitation mean of the previous month and species relative abundance, except in the sea grape forest (Table 1). This may be due this site being mostly a feeding area, since no host plants were found. Thus the presence of butterflies is strongly related with flower availability. Additionally, the presence, in this habitat, of non native plants probably might increase the flower availability annually (Núñez & Barro, 2003), and could be the reason why the rain acts like the primary factor influencing flowering. Although the secondary scrub presents almost the same non native plants as the sea grape forest, there is no correlation of butterfly abundance with rain. It is likely that, in this habitat, flower availability is not the primary factor

Table 1. Values of the Nonparametric Correlation (Spearman r) between relative abundance of the populations (measured as the mean of the major number of individuals in a single count) and precipitation mean of the previous month.

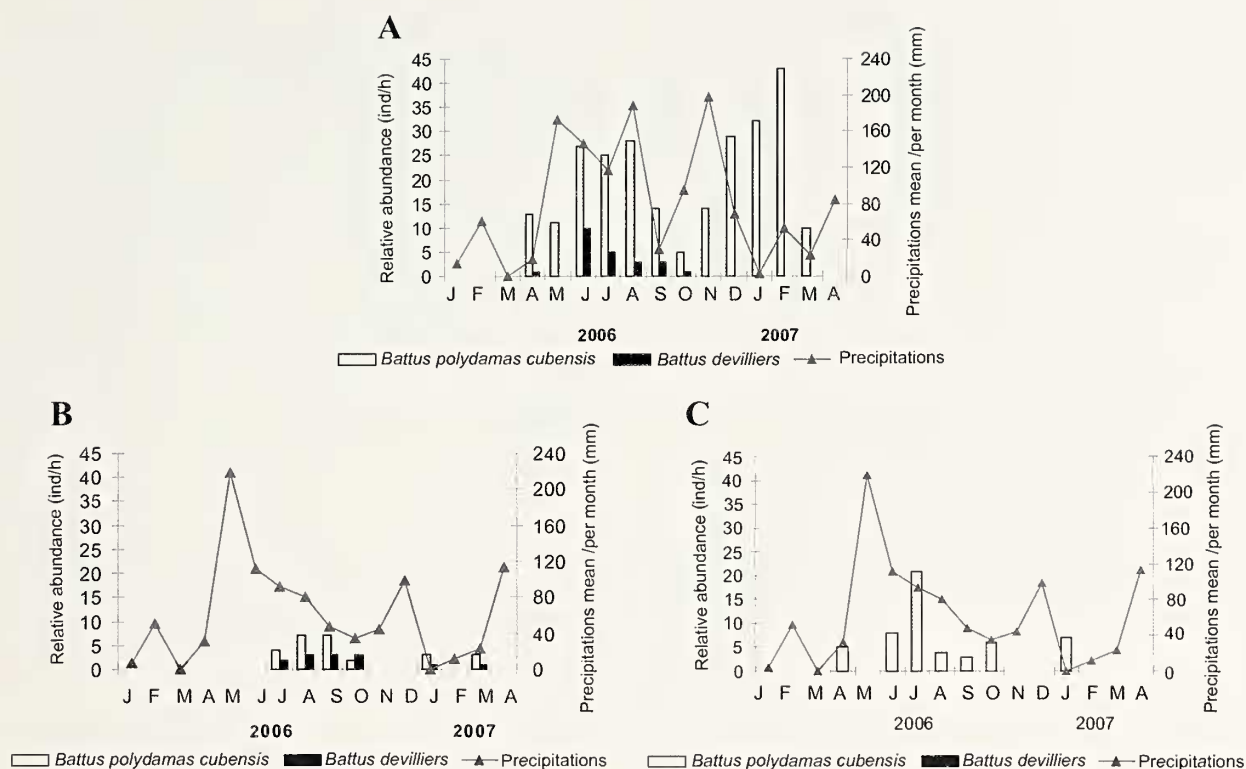| Species/Habitat	Secondary scrub	Evergreen forest	Sea grape forest
Battus polydamas cubensis	0.3082	0.3531	0.6786
Battus devilliers	0.3935	-0.09258	No

Figure 2. Population densities of *Battus devilliers* and *B. polydamas cubensis*, from April, 2006 to March, 2007. **A**: Secondary scrub of Boca de Jaruco. **B**: Evergreen forest of Boca de Canasí. **C**: Sea grape forest of Boca de Canasí. Gray line represents precipitations per month. Black squares represents relative abundance of *Battus devilliers* and the white ones those of *B. polydamas cubensis*. The blank spaces were not sampled. Relative abundance was the highest number of individuals observed in one hour.
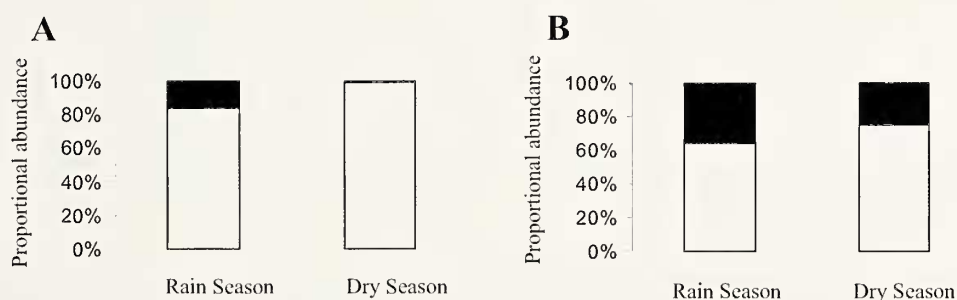

Figure 3. Proportional abundance of *Battus devilliers* and *B. polydamas cubensis* in the habitats in which they coexist. **A**: Secondary scrub of Boca de Jaruco. **B**: Evergreen forest of Boca de Canasí. The black colour represents *Battus devilliers* and white shows *B. polydamas cubensis*.

influencing the abundance of these butterflies. It may be host plant availability, for example.

At Boca de Canasí both species coexist only in the evergreen forest (Fig. 2), thus, no statistical analysis was made for the sea grape habitat. However, nearness of the two sites and the floristic diversity at the latter (Núñez & Barro, 2003) seem to support the idea of delimited feeding and breeding areas for a single population of *B. polydamas cubensis*. In this manner, the sea grape forest may be the foraging area and the evergreen forest the reproductive site (host plants observed only in the latter). This behavior was previously described for a Costa Rican population of this species by Young (1972). It may also explain

the differential abundance of *B. polydamas cubensis* at each habitat, secondary scrub and evergreen forest. Another consequence of the behavior may be the similarity between relative abundance of both species in the evergreen forest during the rainy season (U = 3.5, p = 0.2469) due to an underestimation in counts of the actual number of individuals in the population of *B. polydamas cubensis* (Fig. 4). Data for the dry season were insufficient for analysis.

By contrast, populations of both species in Boca de Jaruco differed significantly (U = 1.5, p = 0.0104) during the rainy season and more so during the dry period (U = 0, p = 0.0022). *Battus devilliers* was always rare compared with *B. polydamas cubensis* (Fig. 4). However, OMR saw both species in equal proportion during the study period at another site approximately 1 km west of transects and nearest to Jaruco River, where native vegetation was best preserved.

Another reason concerning life cycle and reproductive strategy may contribute to the success of *B. polydamas cubensis*. Gregariousness of eggs and larval stages may be the most important because of the benefits described for the behavior as stated by Stamp (1980), Matsumoto (1989) and Reader and Hochuli (2003). Gregarious early stages are absent in *B. devilliers*.

Structural subniche

Sunlight intensity. Large sunny patches are common in Boca de Jaruco due to the presence of abundant herbs and bushes and only few isolated large trees. Accordingly, sunny patches were the category most used in that habitat. The Kruskall-Wallis Test shows differences among the different levels for both species. The Dunn's Multiple Comparisons post test demonstrates that in the morning those differences occur between sunny patches and the other levels (p < 0.001 for both species). During the afternoon differences in the use of three levels were also present. The results of post test were p < 0.001 comparing sunny patches with the other two, although sun filtered and shading patches usage by *B. polydamas cubensis* increases (Fig. 5a, b).

At Boca de Canasí, vegetation cover is more highly developed, so sun filtered and shading patches are more frequent than at Boca de Jaruco. Nevertheless, values of Kruskall-Wallis Test show differences among the mentioned levels. Only *B. devilliers* increased significantly the using of sun filtered sites in the same proportion as sunny patches. Statistical differences were between sunny and shading levels (p < 0.05) and between filtered and shading ones (p < 0.01) in the first hours of day, while during the afternoon the

same relation occurs, but without individuals flying in shading patches (Fig. 5c, d). On the other hand, *B. polydamas cubensis* always preferred sunny patches. Differences in the morning were between first level (sunny) and the filtered and shading patches (p < 0.001 in both cases). During the afternoon no individuals were observed flying in shading patches (Fig. 5c, d).

Our results show that the use of this structural dimension depends not only on habitat, but on the ecological requirements of species. At Boca de Jaruco, sunny sites cover most of the study area and consequently both species made major use of them. Nevertheless, in Boca de Canasí, even when vegetation cover increased in the forest, only *B. devilliers* used filtered patches as well as sunny ones. This tendency matches with the primary habitat of each species, mentioned by Tyler *et al.* (1994), that explains why *B. polydamas* is a widespread and flexible species, whereas *B. devilliers* is sensitive and vulnerable, dependent on forested areas.

Flight stratum

In the morning, at Boca de Jaruco both species mostly fly in the two lower strata (Fig. 6a, b). *Battus devilliers* did not change this strategy during the entire all day, while *B. polydamas cubensis* started to use any stratum indiscriminately after midday. Kruskall-Wallis values were significant in the morning for both species. The post hoc test demonstrated differences between the highest stratum and the lowest one for both species (p < 0.001), and between the intermediate and the highest stratum with p < 0.01 for *B. devilliers* and p < 0.001 for *B. polydamas cubensis*. After midday, KW values did not show any difference among strata used by either species, although graphically we observed that *B. devilliers* keeps similar proportions to those of the morning (Fig. 6a, b).

At Boca de Canasí, there was no difference in flight stratum use during the day. *Battus devilliers* mostly flies in the lowest stratum, with patches of filtered sun. On the other hand, *B. polydamas cubensis* flies in all of the three strata. For *B. devilliers* the post test display differences between the lowest and the intermediate strata with p < 0.01 at both time intervals. Between the lowest and the highest strata we found the same p value for the morning, and p < 0.001 for the afternoon. By contrast, there was no statistical difference in the use of flight stratum by *B. polydamas cubensis* in this habitat (Fig. 6c, d).

Flight strata were more indiscriminately used by both species in the two habitats. The results demonstrate almost no selection for this structural dimension, perhaps because strata are not limiting
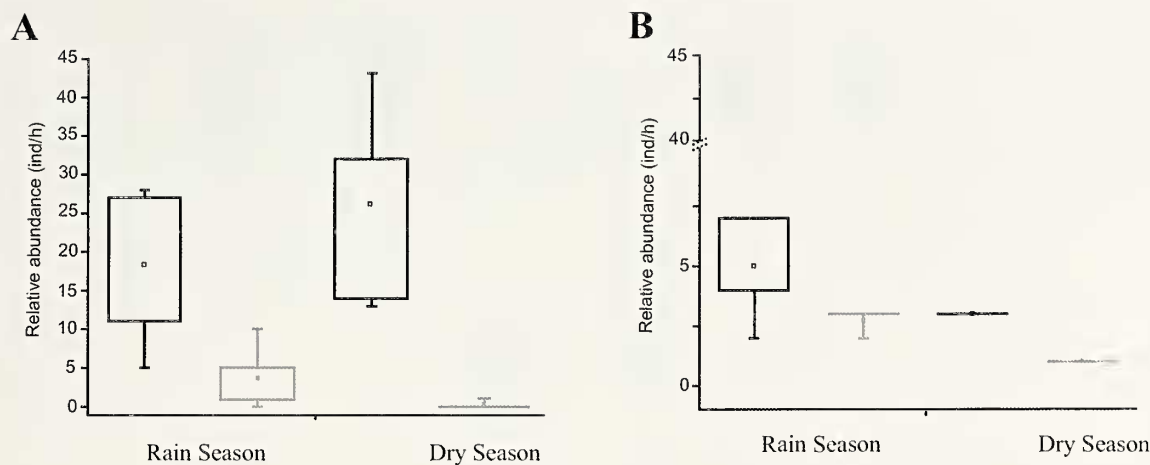
Figure 4. Relative abundance (individuals/hour) of *Battus devilliers* (gray) and *B. polydamas cubensis* (black) in the two seasons defined in Cuba as Rain (May-October) and Dry (November-April). **A**: Secondary scrub of Boca de Jaruco. **B**: Evergreen forest of Boca de Canasí. The graphic represents the median and the 25% and 75% percentils.
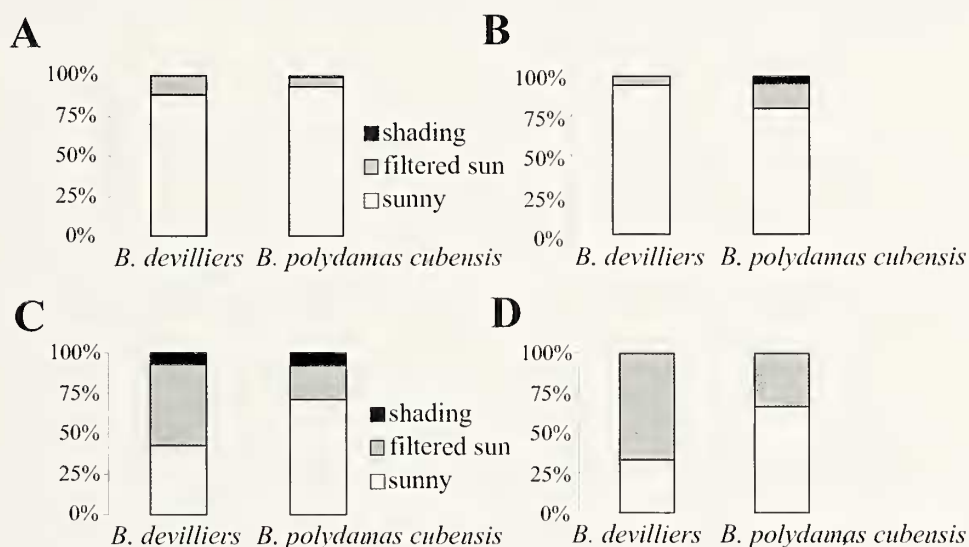

Figure 5. Spacial segregation of *Battus devilliers* and *B. polydamas cubensis* in the structural subniche, specifically in the light intensity used by each one. **A** and **B**: Secondary scrub of Boca de Jaruco (morning and afternoon, respectively). **C** and **D**: Evergreen forest of Boca de Canasí (morning and afternoon, respectively). Analysis only for the rainy season. Morning 9:00 am -11:00 am and afternoon 12:00 pm - 2:00 pm.

resources like flowers and host plant availability or because of low ecological relevance for both species. Similar results were obtained by Fontenla (1989) in a larger butterfly community.

Temporal segregation

Seasonality. Another relevant divergence in population ecology is the seasonal pattern of *B. devilliers* (U = 3.5,

p = 0.0425) by contrast to the continuous dynamics of the other species (U = 10.5, p = 0.2620) (Fig. 2a, b; Fig. 4). This strategy and its presence in all sampled habitats show the greater ecological plasticity of *B. polydamas cubensis*. It is relevant that absence of *B. devilliers* in the sea grape habitat is recent, as five years ago it was observed by Núñez and Barro (2003) and again in lower frequency than *B. polydamas cubensis*. Annual fluctuations of populations, like those
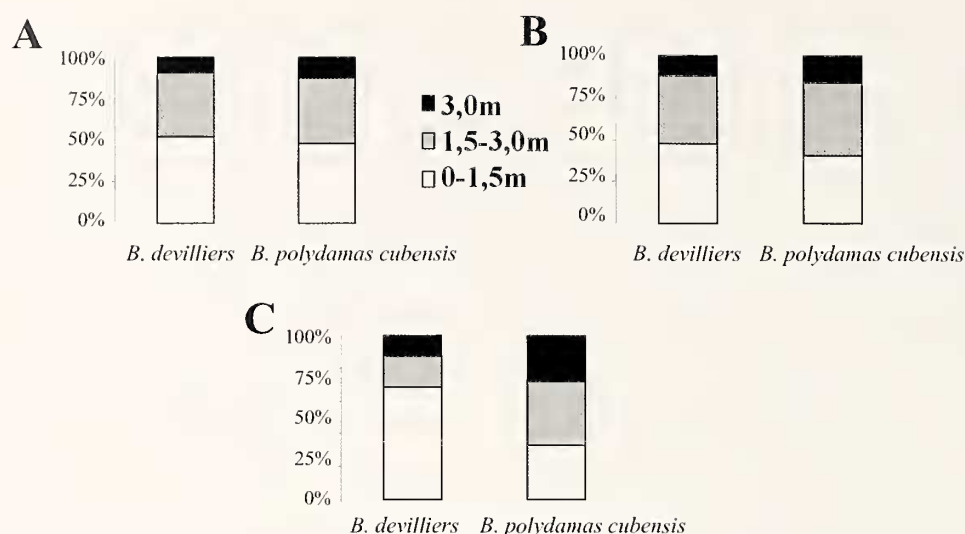
Figure 6. Spacial segregation of *Battus devilliers* and *B. polydamas cubensis* in the structural subniche, specifically in the flight height or stratum used by each. **A** and **B**: Secondary scrub of Boca de Jaruco (morning and afternoon, respectively). **C**: Evergreen forest of Boca de Canasí (there were not found significant differences in both day-hours). It was analized only rain season. Morning 9:00 am - 11:00 am and afternoon 12:00 pm -2:00 pm.
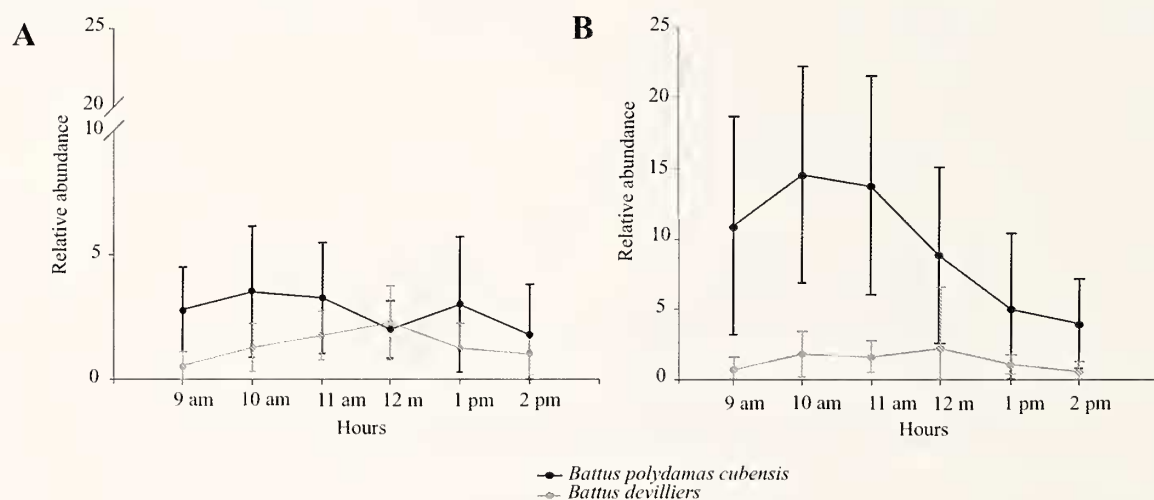

Figure 7. Daily activity of *Battus devilliers* (gray line) and *B. polydamas cubensis* (black line) for the rain season in the two studied habitats. **A**: Evergreen forest of Boca de Canasí. **B**: Secondary scrub of Boca de Jaruco.

observed in past years in Boca de Jaruco by the second author or changes in habitat structure may influence population dynamics.

Daily activity. We analyzed the daily activity for each species and habitat during the rainy season (Fig. 7). Although no statistical analyses were made with these data, two different trends were observed in each population. While the abundance of *B. polydamas cubensis* decreases during the day, with a peak of

activity at 10:00 am, abundance of *B. devilliers* tends to increase until midday with the maximum number of individuals at noon. Thus at 12:00 the means of both populations were similar in the evergreen forest. At the same time, in the secondary scrub of Boca de Jaruco, although the mean values of abundance were so different, the standard deviations were too overlapped. This behavior is not surprising since *B. polydamas cubensis* flies in sunny patches more than

B. devilliers that prefers shade and is less influenced by high temperature of noon. This mechanism may affect thermoregulation permitting the species a longer diurnal flight period.

Battus devilliers and *B. polydamas cubensis* present more selectivity for the dimension sunlight intensity of the structural subniche than for the flight stratum since the late was more indiscriminate used. Temporal segregation seems to occur between these species, *B. devilliers* is influenced by seasonality while *B. polydamas cubensis* is present all the year.

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